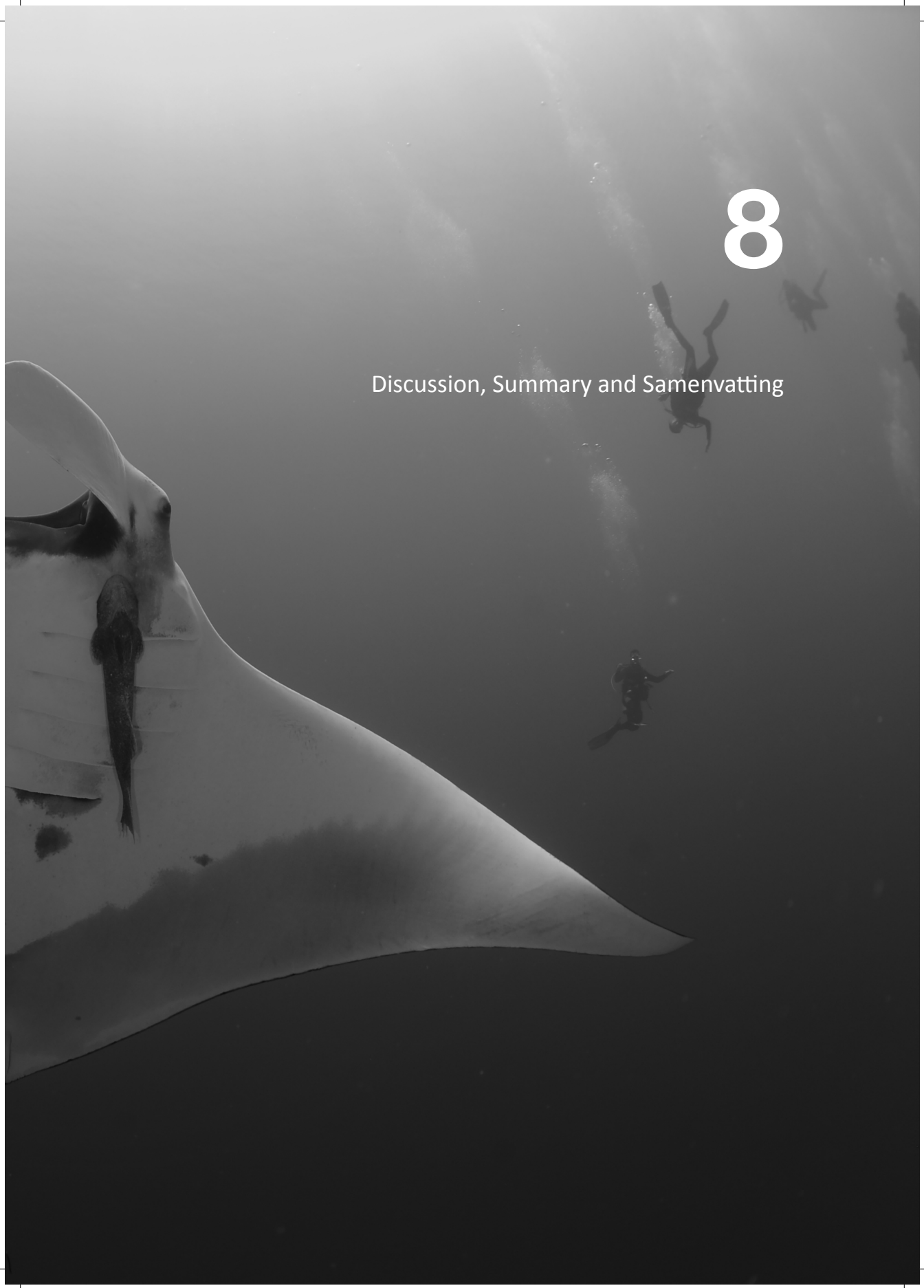
8

Discussion, Summary and Samenvatting



DISCUSSION

What is in a name?

Over the past 20 years our understanding of evolutionary relationships across the tree of life have drastically changed, with the availability of ever-improving molecular phylogenies and more comprehensive sampling (de Queiroz & Gauthier 1990). At the same time, however, branching relationships among clades have shown themselves to be unstable in many cases. For example, higher-level taxonomic groups are often shown to be paraphyletic (or even polyphyletic), i.e. the recognized taxonomic rank only includes a portion of the descendants. Paraphyly most commonly occurs in the tree where taxon sampling has been poor, for example where an "exemplar" approach has been applied in which one individual is used to represent a species, or one species to represent a genus, or one genus to represent a family, etc. Additionally, cryptic species (those that are morphologically indistinguishable but very different at the molecular level) and conversely, morphologically distinctive taxa that are indistinguishable at the molecular level (based on the sequences employed), can also cause paraphyly.

Paraphyly creates nomenclatural problems in the application of Linnaean classification, because the tree of life is based on identity by descent and the recognition of monophyletic groups. The most commonly held view is that a genus or higher-level group should be monophyletic, i.e., a group should contain all species that share the most recent common ancestor (Henning 1966). Therefore, when paraphyly is discovered and confirmed from various data sources, it should be resolved by making nomenclatural changes to the original Linnaean classification. This can be relatively easy to do and if so, should be carried out. If, however, the changes required by nomenclatural priority, as outlined in the Code of Zoological Nomenclature (CZN), result in numerous changes and greater ambiguity in the taxonomy and recognition of the taxon, then measures can be taken to conserve the Latin binomial as a matter of practicality and legality. Indeed, taxonomic stability is a concept that is positively valued in the CZN, and can, in some instances, take precedence over other principles. The importance of a name is more than esoteric. It provides a lingua franca and a legal status that is especially relevant in conservation and species protections.

Results from Chapter 5 indicate that the genus *Mobula* is paraphyletic with respect to *Manta*. The two *Manta* species form a clade together with *Mobula tarapacana* and *Mobula japanica*, a result that is in agreement with previous studies based on molecular data (Aschliman *et al.* 2012a; Aschliman *et al.* 2012b; Naylor *et al.* 2012) and morphology (Adnet *et al.* 2012; Aschliman *et al.* 2012a; Gonzalez-Isais & Dominguez 2004; Herman *et al.* 2000). Based on the principle of monophyly, *Manta* should therefore be renamed to *Mobula*, since *Mobula* (Rafinesque-Schmaltz 1810) has nomenclatural priority over *Manta* (Bancroft 1831). However, it is necessary to consider the practical and legal aspects of a possible name change. Of paramount importance is, in this respect, the issue of conservation. Conservation is based on formal species names, and changing a species' Latin binomial name can potentially influence its conservation status and, as a result, the conservation effort for these vulnerable species.

Manta rays are currently protected in several countries, including Mexico, Ecuador, the Republic of Maldives and the Philippines. Additionally, *Mobula birostris* is listed on Appendix I and II of the Convention of Migratory Species (CMS), and is protected by EU regulations (no. 43/2014), and *M. birostris*, *Mobula alfredi* and the putative third *Manta* species have received protection under the Convention on International Trade in Endangered Species (CITES) Appendix II. It is difficult to predict the consequences of a name change from *Manta* to *Mobula* on each individual conservation measure applicable to *Manta*. However, a review of taxonomic changes and their impact on conservation effort shows that name changes negatively impact conserva-

tion efforts only when they concern threatened species that have been lumped together with a non-threatened species, thereby effectively removing them from any protective category (Morrison *et al.* 2009). For example, the Idaho springsnail (*Pyrgulopsis idahoensis*) was removed from Endangered Species Act (ESA) after it was shown to be conspecific to the more common Jackson Lake springsnail (Hershler & Liu 2004), resulting in decreased conservation efforts. However, it has also been observed that name changes involving iconic species have little effect on conservation effort, even when they concern the lumping of a threatened species with a non-threatened one (Morrison *et al.* 2009). A case-by-case examination of taxonomic changes and their effect on conservation effort does not necessarily prove that renaming *Manta* to *Mobula* would have no impact on conservation effort. However, the iconic status of manta rays, as well as the fact that both manta rays remain "good'" species even if their Latin names are changed, suggests that manta rays will not be negatively impacted if the genus *Manta* ceases to exist.

Species as units of conservation

Knowledge of the full biodiversity of a genus or Family facilitates the identification of appropriate units for conservation and the associated research necessary (Simpfendorfer *et al.* 2011). However, it can also create dilemmas. Based on results from Chapter 5, all of the currently described small (max. DW <130 cm) and morphological similar mobulid species represent distinct evolutionary lineages: First, *Mobula hypostoma* and *Mobula rochebrunei*, which are distributed in the Western and Eastern Atlantic respectively, diverged around 1.1 Mya, and are most closely related to East Pacific *Mobula munkiana*; Second, *Mobula eregoodootenkee* and *Mobula kuhlii*, two small and morphologically similar mobulid species with overlapping distributions in the Indo-West Pacific, diverged more recently at around 500 Kya. These small mobulids are among the least studied species in the Family. With the exception of *M. munkiana*, almost nothing is know about their biology beyond a taxonomic record. Nevertheless, results from Chapter 5 suggest that they are frequently caught in inshore artisanal fisheries and as bycatch in tuna purse seine fisheries (Croll *et al.* submitted), especially across the West Pacific and Indian Oceans (i.e. *M. eregoodootenkee* and *M. kuhlii*). Population trends are unknown, but based on their (likely) limited reproductive potential and high catch rates throughout their ranges, *M. eregoodootenkee* and *M. munkiana* are listed as 'Near Threatened' and *M. rochebrunei* as 'Vulnerable'. *M. kuhlii* and *M. hypostoma* are listed as 'Data Deficient'. More comprehensive threat assessments should be conducted for each of these species separately. Where species overlap in the West Pacific and Indian Oceans, genetic markers developed in chapter 3 and 5 could be used to genotype fisheries catches, as well as dried gill rakers, in order to determine catch rates for each individual species.

M. japanica and *Mobula mobular* represent a different case in which nomenclatural changes could actually worsen protection. The small amount of mitochondrial and nuclear sequence divergence (Chapters 5 and 6) between the two species, as well as placement of *M. mobular* within the Indian/Pacific mitogenome clade of *M. japanica* (Figure 2), strongly suggests that these two taxa are conspecific, i.e., constitute only one species. If genetic and morphological analyses of additional *M. mobular* samples (which are essential in this case where only an "exemplar approach" has been applied) confirm this result, *M. japanica* (Müller & Henle 1841); should be renamed to *M. mobular* (Bonnaterre 1788), since the latter has nomenclatural priority over the former. *M. mobular* only occurs in the Mediterranean Sea and surrounding Atlantic Ocean. It is classified as 'Endangered' on the IUCN Red List, due to unsustainable levels of bycatch in various fisheries (Notarbartolo di Scara *et al.* 2007) and is currently protected in Croatia and Malta, and through the 1995 Barcelona Convention. Unfortunately, merging *M. japanica*

with *M. mobular* will result in a larger group with a greater range, which in turn might result in decreased conservation efforts for *M. mobular* (Morrison *et al.* 2009). If *M. japanica* is indeed synonymized with *M. mobular*, it is of paramount importance that local and regional protective measures for *M. mobular* stay in place and are further expanded.

Populations as units of conservation

At the species level, knowledge of population structure and the overall pattern of genetic diversity allows for the determination of the appropriate geographic scale for conservation management actions. Two types of conservation units (CUs) are most commonly discussed: evolutionarily significant units (ESUs) and management units (MUs) (Moritz 1994b). Although there are many different definitions of ESUs, the term is generally defined as 'a population or group of populations that warrant separate management or priority for conservation because of high genetic and ecological distinctiveness'. At a smaller scale, MUs are populations that are demographically independent within one ESU, and which should be managed separately to ensure the long-term persistence of species.

Based on criteria suggested by Moritz (1994) for the resolution of ESUs and MUs based on genetic markers, *M. japanica* constitutes one ESU, i.e. there are no detectable adaptive differences between lineages within the species (Chapter 6). However, the species does contain several demographically independent populations, which constitute separate MUs (i.e. Atlantic Ocean and Indian/Pacific Ocean populations), and hence should be managed separately to ensure the long-term persistence of species. Limited genetic structure also exists between the East Pacific and Indian/West Pacific Oceans, but it is unclear whether the difference is biologically relevant, due to uncertainty about the reproductive behavior of *M. japanica*, as well as a lack of broader geographic representation of samples from the West Pacific.

The role of upwelling in the evolutionary and demographic history of mobulids

In conjunction with genetic data, palaeoceanographic data provides information about the evolutionary history of a species. A review of the relevant literature suggests that upwelling of deep, nutrient rich water and related high primary productivity played an important role in the rise and subsequent diversification of the mobulid lineage, as well as their historical demography. This is plausible, given the mode of foraging of this species group. Although upwelling is not the only source of high productivity in the ocean, it does concentrate resources in a relatively small geographic area, often providing densities of food particles high enough to meet the large energy demands of filter-feeding marine mega fauna (Croll *et al.* 2005). The importance of upwelling is also evident from the current distribution and migration patterns of mobulids, which for a large part overlap with or follow seasonal upwelling (Anderson *et al.* 2011; Croll *et al.* 2012; Graham *et al.* 2012).

Upwelling is not, however, a stable phenomenon through time, but has waxed and waned following changes in the world's climate throughout the ages. Periods of global cooling have generally been associated with high upwelling intensities (e.g. during the Early and Middle Oligocene), while upwelling has markedly decreased during periods of global warming. Hence, climatic fluctuations have profoundly affected conditions experienced by pelagic marine filter-feeders. In Chapters 5 & 6 I suggest that upwelling has been an important driver of inter- and intra-specific phylogenetic patterns in mobulids:

First, the rise of the mobulid lineage (Chapter 5) around 30 Mya coincided with a period of global cooling (Figure 1), which, together with tectonics-mediated changes in ocean currents, facilitated massive upwelling of nutrient-rich deep waters. This in turn greatly boosted produc-

tivity in tropical and subtropical regions. It is possible that the development of the filter-feeding strategy in mobulids – a key innovation within the Order Batoidae—was mediated by this increase in upwelling, i.e. through ecological opportunity. The upwelling-hypothesis has also been proposed for other large filter-feeders, including mysticeti whales (Fordyce 1980).

Second, later divergences within the mobulid lineage (Chapter 5) largely coincided with periods of global warming (Figure 1), during which upwelling and related primary productivity was generally reduced. This reduction in upwelling would have resulted in the fragmentation of the habitat of filter-feeders, leading to isolation of subpopulations in different regions with limited connectivity between them. If the time of reduced upwelling was sufficiently prolonged, reproductively isolated populations may have diverged enough to evolve into new species. Other (temporary) barriers to dispersal, such as the presence of land-barriers during periods of low sea levels may have further reinforced divergence between species through ecological specialization. Pastene *et al.* (2007) proposed a similar theory for speciation in the minke whales, a temperate baleen filter-feeder.

Third, three of the four mitogenome clades present in *M. japanica* show evidence of demographic expansion during times of increased upwelling during the Pleistocene (Chapter 6). This pattern of expansion is consistent with an overall increase in carrying capacity of existing upwelling regions through increased availability of nutrients, as well as the rise of new upwelling regions. Demographic expansions during the Pleistocene have been observed in various pelagic species and are inferred to be the result of increased upwelling-related primary productivity (Alvarado Bremer *et al.* 2005; Amaral *et al.* 2012; Diaz-Jaimes *et al.* 2010; Duncan *et al.* 2006; Ely *et al.* 2005; Hoelzel *et al.* 2006; Martinez *et al.* 2006; Theisen *et al.* 2008).

How species have responded to past climate fluctuations may provide critical insights about how that species may respond to current climate change (O'Brien *et al.* 2012). Many unknowns remain in projecting the potential effect of climate change on upwelling systems, but based on the IPCC Special Report on Emission Scenario A2, equatorial upwelling systems are projected to decrease by almost 30 % by 2100 (Polovina *et al.* 2011). If correct, such a reduction will have a tremendous impact on mobulids and other filter-feeders that are strongly dependent on the high productivity associated with upwelling. Demographic declines, due to decreased carrying capacity of upwelling regions, as well as major population range shifts to areas with sufficient food availability are projected outcomes.

In conclusion, the high and increasing catch rates in various (bycatch) fisheries, as well as projected contractions of important feeding regions due to climate change pose a formidable threat to the continued existence of this vulnerable group of pelagic elasmobranchs. It is of paramount importance that we act with urgency, before they are lost forever.

Summary

SUMMARY

Mobulids are large pelagic filter-feeders and amongst the most vulnerable of all chondrichthyan species due to slow life histories and extremely low fecundity. Unfortunately, large and expanding fisheries exist in various Asian countries driven by the use of mobulid filter plates in Chinese medicine. Mobulids are also frequently caught as bycatch in tuna purse seine fisheries across their entire range. Due to the low intrinsic growth rate of mobulid populations, even low catch rates can result in significant population declines.

The evolutionary history of mobulid rays has remained enigmatic despite considerable recent interest in mobulid ecology and conservation. This thesis was designed to provide baseline information on mobulid evolution and population genetics, in order to inform mobulid management and better target conservation measures. I used Next Generation Sequencing of entire mitochondrial genomes, conventional Sanger sequencing and supplementary GenBank sequences to reconstruct—for the first time—evolutionary relationships among all currently described mobulid species. I also analyzed intra-specific patterns of genetic variation in one of the most frequently caught species in various fisheries, the circumtropically distributed spinetail devilray, *Mobula japanica*.

The general questions of this thesis were:

1. What are the evolutionary relationships within the Family Mobulidae, and what is the geological timing and pattern of their radiation? What were the probable mechanisms and drivers of mobulid speciation?

2. What is the spatial scale and connectivity of genetically defined populations of the spinetail devil ray, *Mobula japanica*? What were the influences of past climate change on its historical population structure and demography?

3. Is there evidence for sex-biased dispersal in *M. japanica*?

4. What are the main anthropogenic threats to mobulids? How can this group of species be better protected?

The advent of next-generation sequencing (NGS) now makes it possible to cheaply and efficiently obtain large data sets, in comparison with traditional Sanger sequencing or fragment analyses. The application of NGS seems almost endless, and allows for increased resolution in many fields related to biological sciences, including intra- and interspecific studies. For this thesis, the use of mitogenomes resulted in the recovery of highly supported phylogenetic patterns as well as the recovery of four mitogenome clades in *M. japanica*, compared to analyses of individual mitochondrial genes and microsatellites.

Phylogeny of manta and devil rays

Despite the formal separation of mobulids into two genera (i.e. *Manta* and *Mobula*), my research showed that the genus *Mobula* is paraphyletic with the inclusion of *Manta* (Chapter 5). Although paraphyly has been previously suggested based on morphology (Adnet *et al.* 2012; Aschliman *et al.* 2012b; Gonzalez-Isais & Dominguez 2004; Herman *et al.* 2000), parasite evolution (Benz & Deets 1988) and sequence comparisons among a small number of mobulid species (Aschliman *et al.* 2012a; Naylor *et al.* 2012), this is the first time paraphyly has been

confirmed using DNA sequences of all mobulids. My research further showed that mobulids are divided into three distinct clades (Figure 1). Based on a fossil-calibrated phylogenetic analysis, I estimated the rate of mitochondrial evolution in mobulids at 9.93 x 10^{-9} *S* s^{-1} y^{-1}, which is around an order of magnitude slower than rates found in mammals (Martin *et al.* 1992) and concordant with estimates for other chondrichthyan species (Dudgeon *et al.* 2012). Based on this rate, the Family Mobulidae diverged from its closest relatives the cownose rays (Family *Rhinoptera*) during the Oligocene, around 30 Mya. This divergence marked the transition from a durophageous (shell crushing) to a filter-feeding strategy. Subsequent divergences of species occurred during the Early and Middle Miocene (19-17 Mya), followed by long internal branches and a second interval of divergence during the Pliocene and Pleistocene (3.6 Mya – recent) (Figure 1). I speculate that the waxing and waning of upwelling of deep, nutrient rich water, which directly influences the availability of food, has played a large role in the rise and diversification of the mobulid lineage.

Phylogeography and population genetic structure in Mobula japanica

In Chapter 6 I resolved the geographic scale of genetically isolated populations, as well as the demographic history of one of the 11 mobulid species, the circumtropical *M. japanica*. Population genetic structure was assessed using 263 samples from a total of 8 locations from across the Pacific, Indian and Atlantic Oceans, in combination with Sanger sequencing of mitochondrial genes COX1 and NADH5 and 11 microsatellite loci. Results suggested high connectivity across vast oceanic regions. The Atlantic Ocean is genetically differentiated from the Indian and Pacific Oceans (pairwise F_{ST}(msats)=0.033-0.046; pairwise F_{ST}(mtDNA)=0.140-0.167); however, within the Indian and Pacific Oceans, pairwise comparisons showed an absence of population structure. Only hierarchical AMOVA analyses showed weak genetic structure (F_{ST}(msats)=0.007, F_{ST}(mtDNA)=0.048), between two East Pacific regions, and the Atlantic and Indian/West Pacific Oceans. There was no evidence for Isolation by Distance.

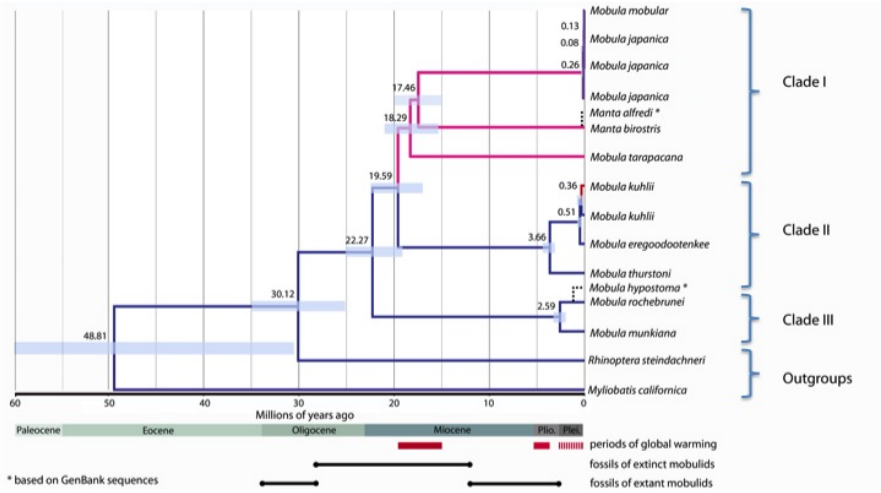


Figure 1: Divergence time estimates based on analysis of the mitogenome BEAST data set. Point estimates of ages are given above each node and transparent blue horizontal bars denote age (95 % highest posterior density). Branch colors show relative nucleotide substitution rates (blue is slow, purple intermediate, red fast). Red bars below the epoch bar denote periods of global warming and associated low upwelling intensities. Black lines below that denote timing of occurrence of extinct and extant mobulid species based on the fossil record.

A review of population genetic structure found in other chondrichthyans suggested that the dispersal capacity of *M. japanica* is only rivaled by the largest of the pelagic sharks, e.g. whale sharks (Castro *et al.* 2007; Vignaud *et al.* 2014) and basking shark (Hoelzel *et al.* 2006). The similarity in population genetic patterns between these species and *M. japanica* was surprising given that both whale and basking sharks are large pelagic species exhibiting trans-oceanic migration (Eckert *et al.* 2002; Gore *et al.* 2008). *M. japanica* on the other hand displays much more limited seasonal migrations: tagging data suggests migrations between the Gulf of California and adjoining East Pacific Ocean, i.e. across distances of <1500 km. Discrepancies between directly observed dispersal distances and indirectly estimated distances based on genetic data are common. Tagging studies follow individuals for months to several years, whereas population genetic studies integrate time across several generations. It is possible that during El Niño years, when upwelling is generally restricted and productivity in regions frequented by *M. japanica* severely reduced (Escribano *et al.* 2004), the species roams across larger distances in search for high productivity feeding regions, thereby promoting connectivity across much larger regions.

In order to gain more potential resolving power for the detection of cryptic population structure, NGS sequencing of whole mitochondrial genomes was applied. This dramatically increased resolution (11,427 bp) compared to the two-gene mtDNA dataset (COX1/NADH5, 1107 bp). Although population genetic patterns based on 60 mitogenome sequences from four locations were similar to patterns based on the more limited datasets, *M. japanica* individuals were separated into four distinct and well-supported mitogenome clades, with clade membership only loosely determined by geographic location (Figure 2) (Chapter 5). Based on sequence divergence and a mitochondrial clock of 9.93×10^{-9} *S* s^{-1} y^{-1}, the four clades diverged during the Late Pleistocene (126 – 11.7 Kya). I hypothesized that this clade structure is the result of vicariance across physical Pleistocene barriers to dispersal, most notably the cold waters around the Cape of Good Hope during periods of low Agulhas leakage (Peeters 2002), exposure of the Sunda/Sahul shelf during LGM low sea level stands (Clark *et al.* 2009). Both of these barriers have been implicated in the formation of mitochondrial clades in other highly vagile tropical pelagic species, for example tuna, billfishes, cetaceans, and some of the larger pelagic shark species (Amaral *et al.* 2012; Bremer *et al.* 1998; Daly-Engel *et al.* 2012; Duncan *et al.* 2006; Martinez *et al.* 2006; Morin *et al.* 2010; Rosel & Block 1996; Vinas *et al.* 2004). The fact that clade membership was only loosely related to geographic sampling location implies the occurrence of periods of increased connectivity between isolated regions, during which mixing of clades occurred. The four mitogenome clades were indistinguishable based on nuclear microsatellite loci, indicating that individuals are interbreeding and therefore belong to the same species. Finally, three of the four clades showed evidence of demographic expansion, which occurred around 40 Kya and between 10 – 25 Kya. Periodic high upwelling and enhanced primary productivity would have increased the carrying capacity for a pelagic filter-feeder.

Sex-biased dispersal

Many chondrichthyan species display philopatric behavior, i.e. a tendency of individuals to return to their natal site or other adopted locality for breeding (Mayr 1963). In chondrichthyans, philopatry is often sex-biased, with females repeatedly returning to specific sites for breeding or pupping, and males roaming more widely (e.g. blacktip sharks, lemon sharks and white sharks, reviewed by Hueter *et al.* 2004). Such behavior, if present, has important implications for the conservation of the species, as nursery areas constitute essential habitats of a population, and are therefore comparable to natal streams for salmon, or nesting beaches for turtles. No reliable information exists about the occurrence of philopatry in *M. japanica*, although catch

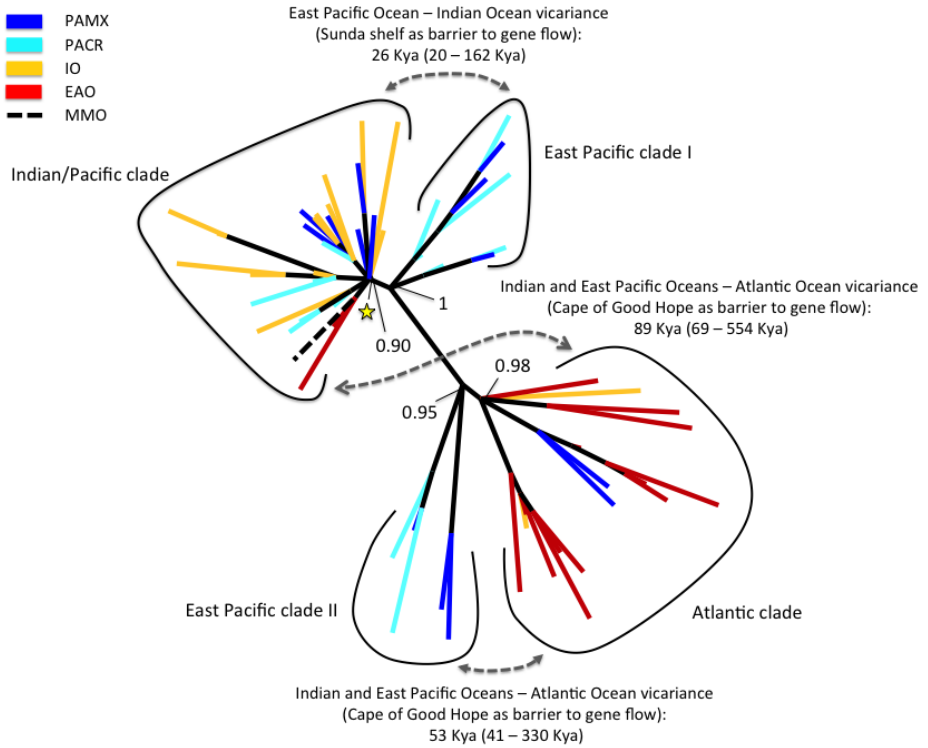


Figure 2: Bayesian phylogenetic tree based on the mitogenome sequences of 60 *Mobula japanica* individuals from Pacific Mexico (PAMX), Pacific Costa Rica (PACR), the Indian Ocean (IO), the East Atlantic Ocean (EAO), one individual of *M. mobular* (MMO), and one individual each of two outgroup species (*M. tarapacana* and *M. birostris*). Branch colors correspond to sampling location. Posterior probabilities (PP) for nodes separating principle clades are shown; all other PP are higher than 0.80 (not shown). Yellow star indicates placement of the outgroup species.

and tagging data suggest that seasonal migration does take place between fixed regions of high primary productivity in the Gulf of California and the surrounding East Pacific Ocean. However, no differences between male and female migration patterns were observed.

Comparisons of genetic markers with uni- and bi-parental inheritance are often used to determine the fidelity of females versus males to particular groupings or locations. Higher pairwise population F_{ST} values based on mitochondrial as opposed to nuclear markers are usually interpreted as philopatric behavior in females. In Chapter 7, female gene flow (based on mitochondrial genes COX1 and NADH5) was compared to female+male gene flow (based on 11 nuclear microsatellites) between the Atlantic and other ocean basins. Results were inconclusive due to wide confidence intervals of microsatellite F_{ST} values. Due to an absence of significant population genetic structure within the Indian and Pacific Oceans, I was also not able to test for the occurrence of sex-biased dispersal in these regions.

Conservation threats and solutions

The attraction of mobulids to plankton-rich habitats and their distribution in the upper water column makes them vulnerable to capture in a wide array of fishing gear, including

recreational and commercial harpoon, gill net, longline, trawl, purse seine and trap fisheries (Chapter 7). Since the 1990's, the market for mobulid filter plates used in Chinese medicine has grown with dried products fetching prices of up to US$71 kg^{-1}. This has led to a rapid expansion of targeted mobulid fisheries, with dried filter plates being exported to mainland China from Sri Lanka, the Philippines, Indonesia and India, where annual catches reach into the tens of thousands (Croll *et al.* submitted). Additionally, bycatch of mobulids in small-scale fisheries has been reported from various countries with, for example, a total of 1,600 mobulids taken in Indonesian skipjack tuna fisheries and around 8,000 individuals in Peruvian artisanal fisheries (Croll *et al.* submitted). In large-scale tuna purse seine fisheries, an estimated total of 13,900 mobulids is caught annually worldwide.

Long-term demographic changes in long-lived pelagic species are difficult to detect (Lewison *et al.* 2004). Time lag, a result of long generation times, can delay the response of a population by many years. Additionally, general difficulties associated with surveys of pelagic animals make the detection of population trends extremely challenging. However, global harvest of mobulids is increasing, and at the same time, decreasing catch rates are reported from various regions. Indeed, population declines have already been reported from several countries, e.g. Mozambique, the Philippines, Indonesia, Mexico and India (Croll *et al.* submitted). As a result, sustainability of current mobulid catch-rates is unlikely.

The pelagic and highly vagile nature of mobulids also impedes conservation efforts. Mobulids roam widely, and may well spend their lives in different exclusive economic zones (and/or the open ocean), where they face a myriad of different threats from targeted and bycatch fisheries. Effective conservation will therefore require coordinated actions by fisheries stakeholders, international trade organizations, non-governmental conservation groups and consumer organizations. Based on the review of the main sources of mortality in mobulids (Chapter 7), three key recommendations have the potential to provide significant conservation benefits:

1. Reduce the demand for filter plates used in Chinese medicine through education and (if necessary) through boycotts and embargos;

2. Reduce bycatch in commercial tuna purse seine fisheries by enforcing fishing prohibitions in important regions such as feeding, breeding and pupping grounds, and by development of net designs that prevent bycatch and/or allow for effective live-release of captured animals;

3. Reduce targeted and bycatch of mobulids in artisanal fisheries through fisheries regulations and technical assistance with gear modification and improvement of live-release techniques.

Samenvatting

SAMENVATTING

Duivelsroggen (de collectieve naam voor *Manta* en *Mobula* roggen van de Familie Mobulidae) zijn grote pelagische planktoneters (filteraars) en behoren, door hun langzame voortplanting en extreem lage vruchtbaarheid, tot de meest kwetsbare haaiachtigen. Helaas bestaat er een intensieve en zich uitbreidende visserij in talloze Aziatische landen, die gedreven wordt door het gebruik van filterplaten in de Chinese Geneeskunde. Duivelsroggen worden ook frequent en over hun hele verspreidingsgebied gevangen als bijvangst in de tonijnvisserij. Door de lage intrinsieke groei van duivelsrogpopulaties kunnen zelfs lage vangsten tot significante negatieve populatietrends lijden.

De evolutionaire geschiedenis van duivelsroggen is lang onduidelijk gebleven, ondanks een recente interesse in de ecologie en bescherming van deze groep roggen. Deze thesis is ontworpen om een basis aan kennis te verwerven over duivelsrog evolutie en populatie genetica, zodat management- en beschermingsmaatregelen beter geïnformeerd en doeltreffender kunnen worden uitgevoerd. Ik heb Next Generation Sequencing (NGS) van hele mitochondriële genomen, conventionele Sanger sequencing en aanvullende GenBank sequenties gebruikt om, voor de eerste keer, de evolutionaire relaties tussen alle momenteel beschreven duivelsroggen te reconstrueren. Ook heb ik patronen in genetische variatie geanalyseerd binnen een van de meest frequent gevangen duivelsroggen, de wereldwijd verspreide gestekelde duivelsrog, *Mobula japanica*.

De belangrijkste vragen in deze thesis waren:

1. Wat zijn de evolutionaire relaties binnen de Family Mobulidae, en wat is de geologische timing en patroon van hun radiatie? Wat zijn waarschijnlijke mechanismen en de drijvende krachten achter Mobulidae soortvorming?

2. Wat zijn de geografische schaal en verbinding tussen genetisch gedefinieerde populaties van de gestekelde duivelsrog, *M. japanica*? Wat waren de invloeden van historische klimaatsverandering op de historische populatie structuur en demografie?

3. Is er bewijs voor verschillende verspreidingspatronen tussen de verschillende geslachten in *M. japanica*?

4. Wat zijn de belangrijkste antropogene dreigingen voor duivelsroggen? Hoe kan deze groep soorten beter beschermd worden?

Door de opkomst van Next Generation Sequencing (NGS) is het nu mogelijk om relatief goedkoop en efficient grotere datasets te genereren, in vergelijking met traditioneel Sanger sequencen of microsatelliet analyse. De bijna onbegrensde mogelijkheden van NGS zorgen voor een ongekende resolutie binnen de biologische wetenschappen, onder andere in intra- en inter-specifieke studies. De toepassing in deze thesis van NGS-gegenereerde mitogenomen zorgde voor zowel sterk onderbouwde fylogenetische patronen, als ook de ontdekking van vier mitogenomische groepen binnen *M. japanica*, in tegenstelling met de toepassing van losse mitochondriële genen en microsatelliet markers.

Fylogenie van duivelsroggen

Ondanks de formele scheiding van duivelsroggen in twee genera (i.e. *Manta* en *Mobula*) heeft mijn onderzoek aangetoond dat het genus *Mobula* parafyletisch is door de toevoeging van *Manta* (Hoofdstuk 5). Alhoewel parafylie van duivelsroggen al eerder was voorgesteld op basis van morfologie (Adnet *et al.* 2012; Aschliman *et al.* 2012b; Gonzalez-Isais & Dominguez 2004; Herman *et al.* 2000), parasitaire evolutie (Benz & Deets 1988) en de vergelijkingen van DNA sequenties van een klein aantal duivelsroggen (Aschliman *et al.* 2012a; Naylor *et al.* 2012), is dit de eerste keer dat parafylie bevestigd is door DNA sequenties van alle duivelsroggen. Mijn onderzoek laat verder zien dat duivelsroggen ingedeeld zijn in drie gemakkelijk te onderscheiden groepen, of 'clades' (Figuur 1). Op basis van een fossiel gecalibreerde fylogenetische analyse schat ik het tempo van de mitochondriële evolutie in duivelsroggen op 9.93 x 10^{-9} nucleotide substituties per jaar per site ($S\ s^{-1}\ j^{-1}$), wat ongeveer een orde van grootte langzamer is dan die in zoogdieren (Martin *et al.* 1992), maar overeenkomt met schattingen voor andere haai-achtigen (Dudgeon *et al.* 2012). Gebaseerd op dit tempo zijn duivelsroggen van de nauwverwante koeneusroggen gedivergeerd tijdens het Oligoceen, ongeveer 30 miljoen jaar geleden. Deze divergentie markeerde de transitie van een durofage (verpletteren van schelpen) naar een filtervoeding leefwijze. Daaropvolgende divergenties van soorten vonden plaats tijdens het Vroege and Midden Mioceen (19-17 miljoen jaar geleden), gevolgd door lange interne takken en een tweede interval van divergentie tijdens het Plioceen en Pleistoceen (3.6 Mya – recent) (Figure 1). Ik speculeer dat opwelling van diep nutriëntrijk water, wat direct de beschikbaarheid van eten beïnvloedt, een belangrijke rol in het ontstaan en divergeren van de duivelsroggen heeft gespeeld (zie hieronder).

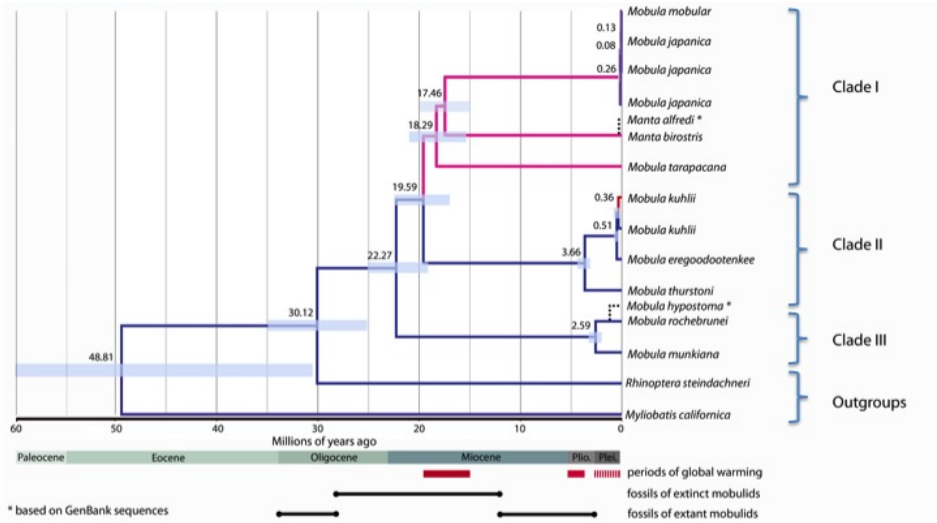
Fylogeography en populatie genetische structuur van Mobula japanica

In Hoofdstuk 6 behandel ik de geografische schaal van genetisch geisoleerde populaties, als ook de demographische geschiedenis van populaties van een van de 11 duivelsroggen, de globaal voorkomende *M. japanica*. Populatie genetische structuur werd geëvalueerd met behulp van 263 individuen uit een totaal aan acht locaties in the Stille, Indische en Atlantische oceanen, in combinatie met Sanger sequenties van mitochondriele genen COX1 en NADH5 en 11 microsatelliet loci. De resultaten suggereren hoge connectiviteit over uitgesrekte oceanische gebieden. De Atlantische Oceaan is welliswaar genetisch gedifferentieërd van de Indische en Stille Oceanen (paarsgewijze F_{ST}(msats)=0.033-0.046; paarsgewijze F_{ST}(mtDNA)=0.140-0.167), maar binnen de Indische en Stille Oceanen lieten analyses zien dat er geen populatie structuur aanwezig is. Alleen een hiërarchische AMOVA analyse resulteerde in een zwakke genetische structuur (F_{ST}(msats)=0.007, F_{ST}(mtDNA)=0.048) tussen twee populaties uit de Oostelijke Stille Oceaan, en tussen de Atlantische en de Indische/Stille Oceanen. Er was geen bewijs voor isolatie door afstand (Isolation by Distance).

Een samenvatting van populatiestructuur in andere haaiachtigen suggereert dat de migratiecapaciteit van *M. japanica* alleen wordt overtroffen door die van de grootsten van de pelagische haaien, de walvishaai (Castro *et al.* 2007; Vignaud *et al.* 2014) en de reuzenhaai (Hoelzel *et al.* 2006). De gelijkenis in populatiestructuur tussen deze soorten en *M. japanica* was verassend, gezien dat zowel bij de walvishaai als de reuzenhaai transoceanische migraties voorkomen (Eckert *et al.* 2002; Gore *et al.* 2008). *M. japanica* daarentegen laat veel kortere seizoensgebonden migratie zien: satellietzender data suggereert migratie tussen de Golf van California en de aangrenzende Oostelijke Stille Oceaan, over een afstand van minder dan 1500 km. Discrepanties tussen direct waargenomen migratieafstanden en indirect geschatte afstanden gebaseerd of genetische data zijn gebruikelijk. Satellietzender studies volgen individuen gedurende maan-

den tot jaren, terwijl populatie genetische data verschillende generaties beschrijven (tientallen jaren). Het is mogelijk dat gedurende El Niño jaren, wanneer opwelling in de gebieden waar *M. japanica* frequent voorkomt zwaar gereduceerd is, de soort over veel langere afstanden zwemt naar gebieden met hogere productie, waardoor migratie over wijd uit elkaar liggende regios gepromoot wordt.

In een poging eventuele verborgen populatie structuur zichtbaar te maken zijn hele mitochondriële genomen gesequenced met behulp van NGS. Dit verhoogde de resolutie dramatisch (11,427 bp) in vergelijking tot de twee-gen mtDNA dataset (COX1/NADH5, 1107 bp). Alhoewel populatie genetische patronen in de mitogenomen overeenkwamen met die gebaseerd op de kleinere dataset, zijn *M. japanica* individuen verdeeld in vier groepen, waarbij groepslidmaatschap maar in kleine mate bepaald is door locatie van herkomst (Figuur 2) (Hoofdstuk 5). De vier groepen zijn waarschijnlijk gedivergeerd tijdens het Late Pleistoceen (126 –11.7 Kya), gebaseerd op sequentie divergentie en een mitochondriele klok van $9.93x10^{-9}$ *S s*$^{-1}$ *j*$^{-1}$. Ik speculeer dat deze groepsstructuur het resultaat is van divergentie door fysieke migratie barrières die in het Pleistoceen aanwezig waren, zoals de koude wateren rond de Kaap de Goeie Hoop tijdens perioden van lage 'Agulhas leakage' (Peeters 2002), en de Sunda/Sahul landbrug tijdens de laatste ijstijd (Clark *et al.* 2009). Beide barrières zijn eerder al geïmpliceerd in de formatie van mitochondriële groepen in andere migrerende tropische pelagische soorten, bijvoorbeeld in tonijnen, zwaardvissen, cetaceeën en in sommige van de grotere pelagische haaiensoorten (Amaral *et al.* 2012; Bremer *et al.* 1998; Daly-Engel *et al.* 2012; Duncan *et al.* 2006; Martinez *et al.* 2006; Morin *et al.* 2010; Rosel & Block 1996; Vinas *et al.* 2004). Het feit dat groepslidmaatschap maar losjes gebaseerd was op geografische locatie van herkomst impliceert periodes van

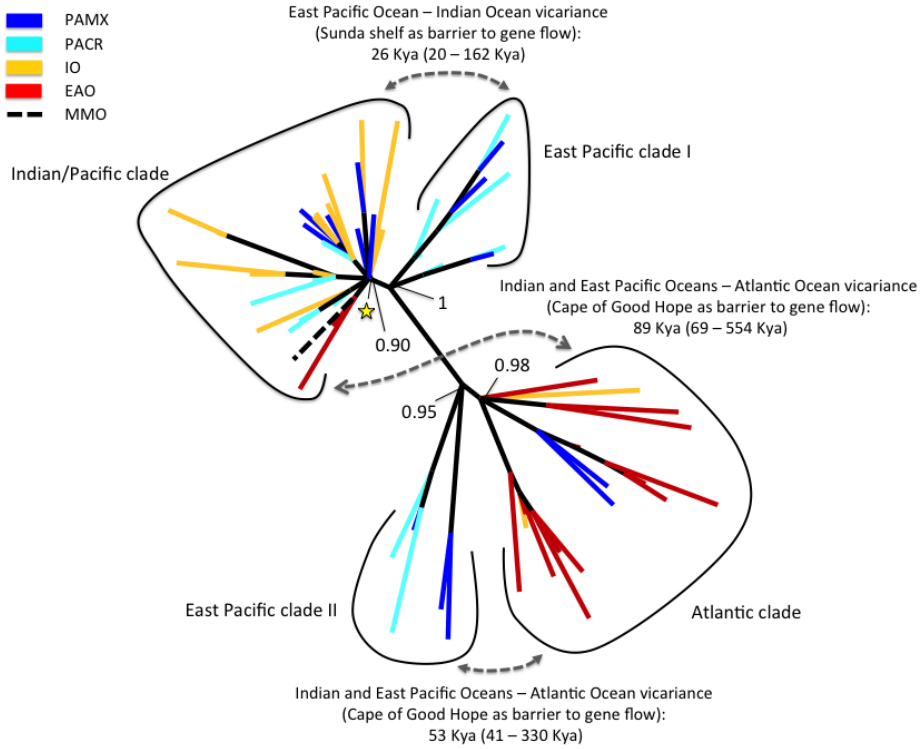


Figuur 1: Divergentietijd schattingen op basis van een analyse van mitogenomen. Puntschattingen van divergentietijden zijn aangegeven boven elk knooppunt, en transparante blauwe horizontale strepen indiceren tijd (95% highest posterior density). Kleuren van lijnen tussen taxa laten de relatieve snelheid van nucleotidesubstitutie zien (blauw is langzaam, paars is gemiddeld, rood is snel). Rode strepen onder de tijdperkenbalk illustreren perioden van klimaat warming and geassocieerde lage opwelling intensiteiten. De zwarte lijnen daaronder geven de timing van het voorkomen van uitgestorven en bestaande duivelsrogsoorten weer, gebaseerd op fossielen.

hoge connectiviteit tussen geïsoleerde regio's, waarbij de verschillende mitogenoomgroepen zich weer mengden. De vier groepen waren niet te onderscheiden van elkaar op basis van microsatelliet loci, wat impliceert dat individuen van verschillende groepen tot dezelfde soort behoren. Verder lieten drie van de vier groepen bewijs van demografische expansie zien, rond 40 duizend jaar geleden, en tussen 10-25 duizend jaar geleden. Perioden van toenemende opwelling en een daarmee samenhangende hoge primaire productie die onder invloed van het klimaatsveranderingen voorkwamen, zouden gezorgd kunnen hebben voor verhoogde draagkracht voor een pelagische planktoneter.

Geslachts-afhankelijke verspreiding

Veel haaiachtigen vertonen filopatrisch gedrag, wat inhoudt dat individuen terugkeren naar de plek van geboorte of een andere geadopteerde locatie om zich voort te planten (Mayr 1963). Zulk gedrag is bij haaiachtigen vaak geslachts-gebonden, waarbij vooral het vrouwelijke geslacht herhaaldelijk terugkeert naar specifieke locaties voor reproductie of om jongen te werpen, terwijl het mannelijke geslacht over veel grote gebieden migreert (bijvoorbeeld zwartpunthaaien, citroenhaaien en witte haaien, samengevat door Hueter *et al.* 2004).



Figuur 2: Bayesian fylogenetische boom gebaseerd op mitogenoomsequenties van 60 *Mobula japanica* individuen uit Mexico (Stille Oceaan, PAMX)), Costa Rica (Stille Oceaan, PACR), de Indische Oceaan (IO), de Oostelijke Atlantische Oceaan (EAO), een *Mobula mobular* individu (MMO), en een individu van elk van de twee 'outgroup' soorten (*Mobula tarapacana* en *M. birostris*). De kleur van ijnen correspondeert met locatie van herkomst. Posterior probabilities (PP) voor knooppunten die de groepen van elkaar scheiden staan vermeld; alle andere PP zijn hoger dan 0.80 (niet vermeld). De gele ster indiceert de positie van de outgroup soorten.

Filopatrisch gedrag heeft belangrijke implicaties voor het behoud van een soort, omdat voorplantings- en geboortegronden belangrijke habitats vormen voor een populatie, zoals ook geboorterivieren voor zalmen en broedstranden voor zeeschildpadden. Er bestaat geen betrouwbare informatie over het verschijnsel filopatrie in *M. japanica*, maar vangst- en satellietzenderdata suggereren dat seizoensgebonden migratie plaatsvindt tussen regio's van hoge productiviteit in de Golf van California en de aangrenzende Oostelijk Stille Oceaan. Er zijn echter geen verschillen tussen de geslachten geobserveerd.

Vergelijkingen tussen genetische markers met alleen vrouwelijke (mitochondrieel DNA), en met zowel mannelijke als vrouwelijke overerving (nucleair DNA) worden vaak gebruikt om te bepalen of een geslacht van een soort meer trouw is aan een bepaalde groep of locatie. Hogere paarsgewijze populatie F_{ST} waarden gebaseerd op mitochondriële versus nucleaire markers worden gewoonlijk geïnterpreteerd als filopatrisch gedrag in de vrouwelijke sekse. In Hoofdstuk 7 wordt de uitwisseling van vrouwelijke genen (gebaseerd op mitochondriële genen COX1 en NADH5) vergeleken met genen die door beide geslachten worden doorgegeven (de 11 nucleaire microsatellieten), tussen de Atlantische en andere Oceanen. Resultaten waren niet eenduidig door de wijde betrouwbaarheidsintervallen van de microsatelliet F_{ST} waarden. Door de absentie van significante populatiestructuur binnen de Indische en Stille Oceanen was het ook niet mogelijk om de aanwezigheid van filopatrisch gedrag in deze regio's te onderzoeken.

Behoud van duivelsroggen: problemen en oplossingen

De aantrekkingskracht van planktonrijke gebieden op duivelsroggen, samen met hun distributie in de bovenste waterkolom, maken deze soorten uiterst kwetsbaar voor een groot aantal verschillende visserijen, onder andere recreatieve en commerciële harpoenvisserij, kiewnetvisserij, langlijnvisserij, trawlervisserij, ringzegenvisserij en kooivisserij (Hoofdstuk 7). De markt voor filterplaten van duivelsroggen, welke gebruikt worden in de Chinese Geneeskunde, is sterkt gegroeid sinds 1990, en prijzen voor gedroogde producten liggen nu rond de €65 per kilo. Dit heeft geleid tot een snelle expansie van een gerichte duivelsrogvisserij in Sri Lanka, de Filipijnen, Indonesië en India, vanwaar gedroogde filterplaten worden geëxporteerd naar het Chinese vasteland (Croll *et al.* Submitted). In de ringzegenvisserij naar tonijn worden ook nog eens gemiddeld 13,900 duivelsroggen per jaar gevangen.

Het is moeilijk om langdurige veranderingen in de demografie van langlevende soorten te detecteren. Als resultaat van de lange generatietijd kan verhoogde mortaliteit pas na vele jaren een effect geven. Ook is het, door de enorme uitgestrektheid en ontoegankelijkheid van de pelagische habitat over het algemeen moeilijk om populatietrends in zulke soorten te onderzoeken. Toch is het duidelijk dat de globale oogst van duivelsroggen toeneemt, terwijl tegelijkertijd de vangstratio's in uiteenlopende gebieden omlaag gaan. Negatieve populatietrends zijn daadwerkelijk waargenomen in verschillende landen, onder andere Mozambique, de Filipijnen, Indonesië, Mexico en India (Croll *et al.* Submitted). Het is daarom onwaarschijnlijk dat de huidige vangst van duivelsroggen duurzaam is.

De pelagische en de vrij-zwemmende natuur van duivelsroggen zorgt voor meer problemen omtrent het behoud van deze groep. Duivelsroggen hebben een wijd verspreidingsgebied, en het is daarom mogelijk dat ze hun leven binnen verschillende exclusieve economische zones (en/of de open oceaan) doorbrengen, waar ze potentieel in aanraking komen met bedreigingen van gerichte- of bijvangst visserijen. Effectief behoud van deze groep vraagt daarom gecoördineerde acties van visserijaandeelhouders, internationale handelsorganisaties, natuurbehoud groepen en consumentenorganisaties. Gebaseerd op een samenvatting van de belangrijkste sterfteoorzaken in duivelsroggen (Chapter 7) kunnen drie aanbevelingen gegeven worden die potentieel het behoud van deze soorten ten goede komen:

1. Reduceer de vraag naar filterplaten vanuit Chinese Geneeskunde, door educatie en (zo nodig) door boycots en embargo's;

2. Reduceer bijvangst in de commerciële ringzegenvisserij naar tonijnen, door het afdwingen van een verbod op visserij in belangrijke regio's, zoals foerageer-, voortplantings- en geboortegronden, en door netten te ontwikkelen die bijvangst voorkomen en/of toestaan dat dieren op een effectieve manier levend vrijgelaten kunnen worden.

3. Reduceer gerichte- en bijvangst van duivelsroggen in kleinschalige visserij door regelgeving, en door technische assistentie te verlenen met de modificatie van vistuig en het verbeteren van technieken om dieren levend vrij te laten.

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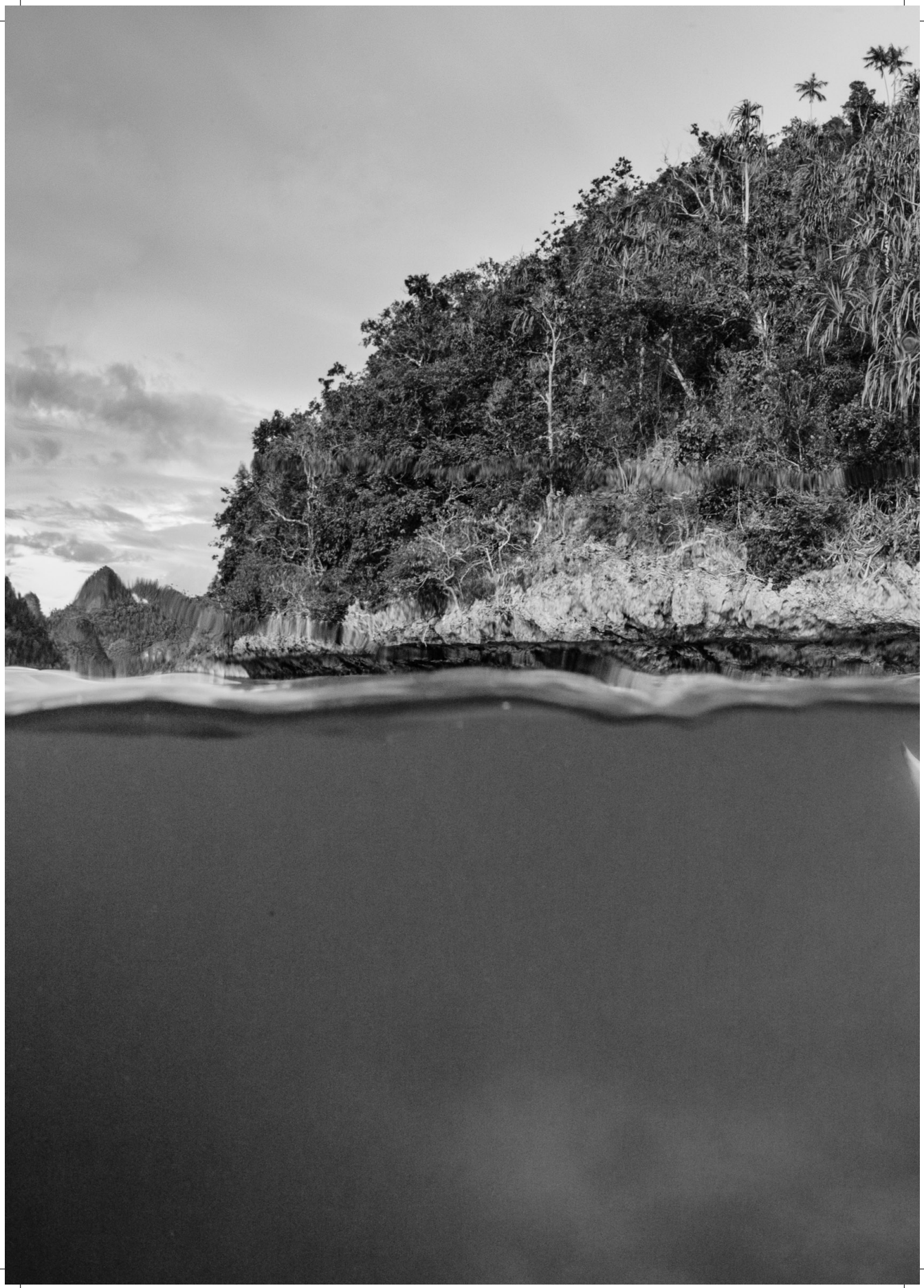

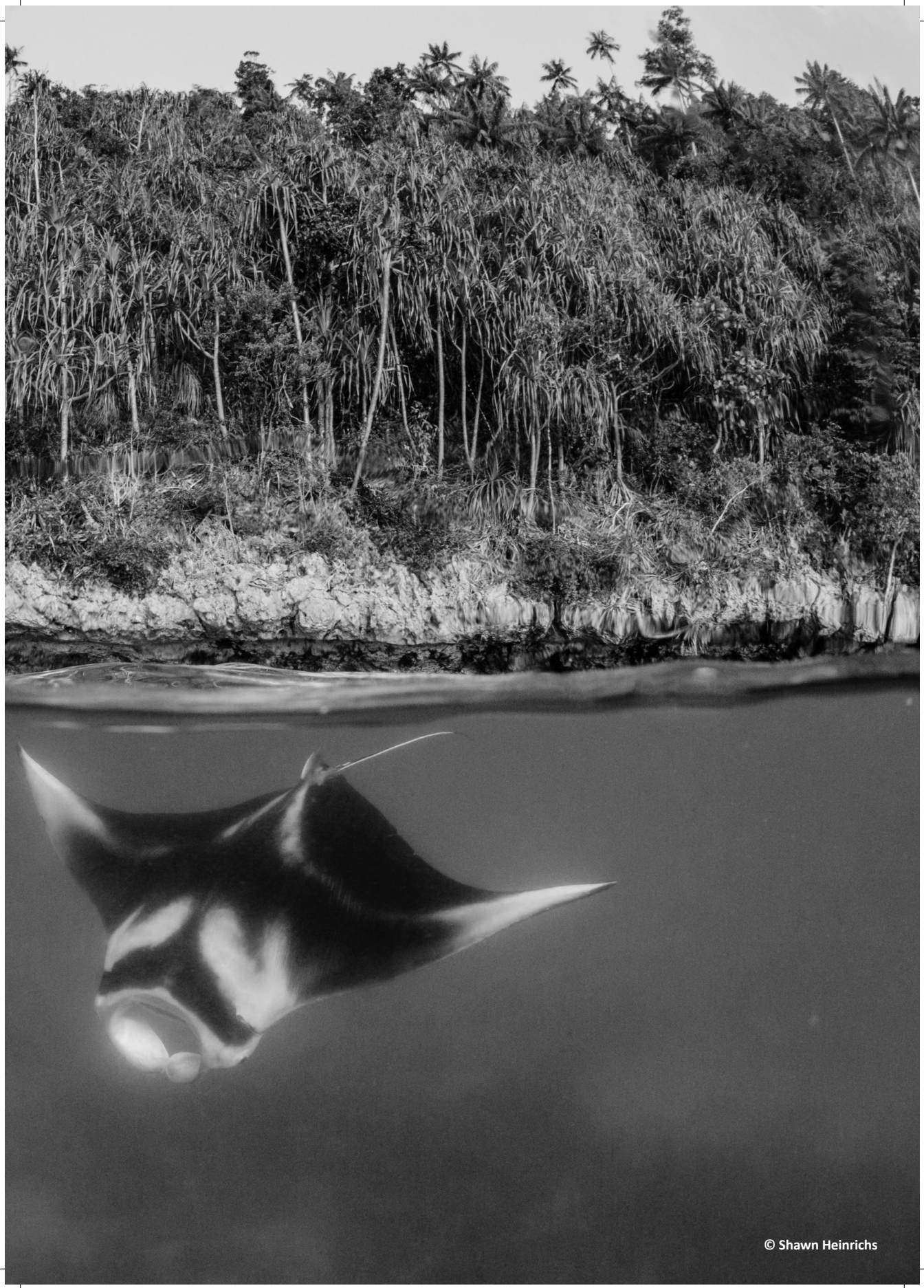
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